



Spatial variation in reproductive effort of a southern Australian seagrass



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ABSTRACT

In marine environments characterised by habitat-forming plants, the relative allocation of resources into vegetative growth and flowering is an important indicator of plant condition and hence ecosystem health. In addition, the production and abundance of seeds can give clues to local resilience. Flowering density, seed bank, biomass and epiphyte levels were recorded for the temperate seagrass *Zostera nigricaulis* in Port Phillip Bay, south east Australia at 14 sites chosen to represent several regions with different physicochemical conditions. Strong regional differences were found within the large bay. Spathe and seed density were very low in the north of the bay (3 sites), low in the centre of the bay (2 sites) intermediate in the Outer Geelong Arm (2 sites), high in Swan Bay (2 sites) and very high in the Inner Geelong Arm (3 sites). In the south (2 sites) seed density was low and spathe density was high. These regional patterns were largely consistent for the 5 sites sampled over the three year period. Timing of flowering was consistent across sites, occurring from August until December with peak production in October, except during the third year of monitoring when overall densities were lower and peaked in November. Seagrass biomass, epiphyte load, canopy height and stem density showed few consistent spatial and temporal patterns. Variation in spathe and seed density and morphology across Port Phillip Bay reflects varying environmental conditions and suggests that northern sites may be restricted in their ability to recover from disturbance through sexual reproduction. In contrast, sites in the west and south of the bay have greater potential to recover from disturbances due to a larger seed bank and these sites could act as source populations for sites where seed production is low.

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1. Introduction

Flower and seed production are integral features of plant life histories, contributing to population maintenance and genetic diversity. Flowering intensity, timing and subsequent seed bank abundance and persistence influence the health and resilience of plant populations, providing mechanisms for annual regeneration, recovery from disturbances, dispersal and genetic diversity. Flowering and seed densities vary spatially and temporally depending on local environmental conditions and genetic adaptations (Elzinga et al., 2007; Fenner and Thompson., 2005).

Seagrasses are marine angiosperms that reproduce sexually through the production of seeds and asexually through rhizome extension and vegetative fragments. Seagrass seeds are produced through the development of flowers and subsequent release of hydrophilic pollen specifically adapted to the marine environment (Les, 1988). Life history and reproductive strategies vary widely between seagrass species; from annual species that rely heavily on seed banks (e.g. *Halophila decipiens*, Hammerstrom et al., 2006), to long lived species that rarely produce flowers (e.g. *Posidonia oceanica*, Arnaud-Haond et al., 2012; Diaz-Almela et al., 2006), and also include the production of vegetative fragments that act as a form of dispersal (e.g. *Zostera nigricaulis*, Cambridge et al., 1983; Thomson et al., 2015). Seeds were traditionally thought to play a relatively minor role in the regeneration and recovery of seagrass (Den

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Hartog, 1970; Les, 1988), but recent genetic studies have shown sexual reproduction to be an important contributor to patch persistence and growth (Becheler et al., 2010; Jarvis and Moore, 2010; Sherman et al., 2016; Waycott et al., 1997). Seeds also contribute significantly to seagrass dispersal and gene flow (Kendrick et al., 2012; Ruiz-Montoya et al., 2015). Dispersal potential of seeds varies widely among seagrass species; many species (e.g. *Posidonia*, *Thalassia*) produce positively buoyant seeds that can be disperse hundreds of kms on ocean currents, while other species (e.g. *Zostera*) hard negatively buoyant seeds that typically disperse only short distances from the parental plant, but can be dispersed more widely if attached to floating fragments (Furman et al., 2015; Kendrick et al., 2012; McMahon et al., 2014; Ruiz-Montoya et al., 2015; Weatherall et al., 2016).

For species with negatively buoyant seeds (e.g. *Zostera*), seeds primarily contribute to the local seed bank with few seeds dispersing greater than 10 m (Furman et al., 2015; Zipperle et al., 2009). Seed banks provide a mechanism to contend with major environmental change by harbour significant genetic diversity and enabling populations to survive unfavourable conditions. They also allow for a more rapid recovery when vegetative recovery is absent or slow (Hammerstrom et al., 2006; Jarvis and Moore, 2010; Zipperle et al., 2009). Therefore, maintaining healthy viable seed banks is important for the persistence of seagrass populations.

Zostera nigricaulis is a perennial monoecious seagrass that forms large subtidal beds in coastal bays and inlets of southern Australia (Jacob and Les, 2009; Kuo, 2005). Inconspicuous spathes containing 2–6 male and female flowers develop on the shoots of *Z. nigricaulis* leaves from September to February, producing small, negatively buoyant, ovoid seeds (Kuo, 2005), while asexual growth occurs through rhizome extension and production of vegetative propagules (Cambridge et al., 1983; Thomson et al., 2015). Within most sheltered embayments of south-eastern Australia, *Z. nigricaulis* is the dominant structured habitat, forming large subtidal beds that fluctuate in area over time (Ball et al., 2014; Hirst et al., 2016). These beds are an important habitat for a range of fauna (Murphy et al., 2010; Smith et al., 2008) and perform a number of ecosystem functions including sediment stabilisation and carbon sequestration (Macreadie et al., 2014b).

Despite the importance and prevalence of *Z. nigricaulis* as a habitat forming species, little is known about its basic life history and like other seagrass species there is a lack on empirical knowledge regarding the spatial and temporal dynamics of flowering and seed production (York et al., 2016). The few studies that have investigated *Z. nigricaulis*, or *Heterozostera tasmanica* as it was formerly known (Coyer et al., 2013; Jacob and Les, 2009; Kuo, 2005), have shown morphological and reproductive characteristics can vary in space and time (Bulthuis and Woelkerling, 1983b; Campey et al., 2002). Growth rate and morphology of *H. tasmanica* vary spatially in Victoria (Bulthuis and Woelkerling, 1983b) and flowering of *H. tasmanica* occurred in only 1 of 3 years on Success Bank in Western Australia (Campey et al., 2002). Similarly, other seagrasses such as the closely related *Z. muelleri* can vary in morphology and reproductive effort at small spatial scales including across the intertidal zone (Conacher et al., 1994; Ramage and Schiel, 1998). The reasons for this variation are unclear but may include differences in environmental conditions such as temperature (Potouroglou et al., 2014) or epiphyte cover which can restrict photosynthetic rate and production via shading (Bulthuis and Woelkerling, 1983a; Orth and Van Montfrans, 1984).

Here, we describe variation in reproductive effort and several other demographic variables for *Z. nigricaulis* from several sites within a large temperate embayment, Port Phillip Bay, Victoria, Australia, which shows considerable spatial variation in a range of physicochemical variables. We aimed to 1) identify the flowering

period of *Z. nigricaulis*, and 2) describe variation in flower and seed production, and, seagrass morphological characteristics (canopy height, above and below ground biomass, epiphyte biomass, and stem density) across Port Phillip Bay, to determine whether variation occurs at the regional scale, or more reflects conditions within local seagrass habitats.

2. Methods

2.1. Site

Port Phillip Bay is a large semi-enclosed bay in south eastern Australia, covering approximately 1900 km² with a coastline of 325 km. Port Phillip Bay is generally shallow (average depth 14 m) and is joined to Bass Strait through a narrow (3.4 km wide) channel. Seagrass is a major habitat in the bay with *Z. nigricaulis* as the dominant subtidal seagrass and is common in the south and west of the bay to depths of 7 m (Ball et al., 2014). Total *Z. nigricaulis* cover within Port Phillip Bay fluctuates considerably over time and has shown a recent decline (Ball et al., 2014). To gain an estimation of *Z. nigricaulis* seed bank and flowering intensity, an initial survey was undertaken in October 2011 where samples were collected from 14 sites in 6 regions across the bay (Fig. 1). We defined 6 regions, based on hydrodynamics, sediments, and nutrient conditions (Table 1): Swan Bay (North Swan Bay, South Swan Bay), South (Blairgowrie, Rosebud), North (Altona, Jawbone, Ricketts Point), Central (Edwards Point, Mud Islands), Outer Geelong Arm (Kirk Point, Point Richards) and Inner Geelong Arm (Avalon, Grand Scenic, Point Henry).

Monitoring continued at one site within each region to determine the consistency of flowering and persistence of the seed bank, with the exception of Central Port Phillip Bay, which was not sampled again due to problems gaining access to the site. Samples were collected every three months from October 2011 until January 2014 with additional above ground samples taken each month between July and January each year to assess flowering intensity at Altona, Blairgowrie, Point Henry, Point Richards and South Swan Bay (Smith et al., 2016).

2.2. Sampling design

At each site, 3 replicate quadrats were haphazardly thrown within three permanent 10 × 10 m plots, 50–100 m apart (n = 9) and sampled. Plots were located at the interior of patches, and gaps in cover avoided to ensure consistency within sites. Samples consisted of a 0.25 × 0.25 m quadrat where canopy height (the highest point of the canopy in cm) was measured and all seagrass cut at the sediment and collected. A 10 cm diameter corer was then used to take a 10 cm deep core within the cleared area. Above ground samples were frozen and below ground refrigerated prior to being processed in the laboratory. Below ground samples were processed within 3 weeks to ensure seed viability was not affected by refrigeration. Above ground samples from Point Henry in January 2013 and below ground from Blairgowrie and quadrat 1 at Point Henry in October 2013 were not collected due to poor weather.

2.3. Laboratory processing

2.3.1. Below ground samples

Cores were sieved through a 2 mm and 710 μm sieve to separate below ground biomass, seeds and sediment. Reproductive effort was estimated by examining material from the 710 μm sieve for seeds to determine seed density across sites and regions. Under a dissecting microscope all seeds were removed, tested for viability

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